

Wende hinaus in den annähernd unverändert, d. h. kontinental gebliebenen Gebieten Eurasiens fortleben konnten. *Arvicola antiquus* ist z. B. bisher in England, Frankreich, Süddeutschland und vielleicht auch Niederösterreich nachgewiesen worden (HEIM DE BALSAC u. GUISLAIN 1955; HINTON 1926; WETTSTEIN 1938). Das bedeutet gleichzeitig, daß diese Arten ihren ökologischen Charakter im Jungpleistozän hier bei uns erworben haben müssen. Bei Maulwürfen und Hamstern liegen schon in älteren Abschnitten des Pleistozäns Riesenformen (*Talpa episcopalis*, *Cricetus runtonensis*) neben "normalwüchsigen" vor. Ihre stammesgeschichtlichen Beziehungen zu den jungpleistozänen Großformen sind noch in der Diskussion, doch könnte man gegebenenfalls in ihrer Körpergröße eine Präadaptation an die kaltzeitlichen Bedingungen des Hoch- und Spätwürm vermuten.

Abschließend sei noch folgendes betont: Die im vorstehenden erörterte biologische Caesur am Ende der Eiszeit ist nur lokal zu betrachten. Auch innerhalb des Untersuchungsgebiets wird sie — etwa im Süden und Norden — nicht absolut zeitgleich gewesen sein und offenbart sie sich z. B. im Auftreten einzelner Arten differenziert in den verschiedenen Fundstellen. Eine Verknüpfung mit der glazialgeologischen Gliederung schließlich ist sehr problematisch, denn Gletscher und Tiere können bei Klimaschwankungen ganz unterschiedlich schnell reagiert haben.

Zusammenfassung

Der Klimawechsel an der Pleistozän-Holozän-Grenze war im Untersuchungsgebiet besonders schnell und einschneidend. Die Kleinsäugerfauna dieses Zeitbereichs läßt sich in drei Gruppen aufteilen:

1. Arten der jungpleistozänen Kaltsteppen. Sie bestehen in kontinentalen Gebieten der Holarktis noch heute. Von dort aus wanderten sie bei uns ein und dort hatten sie ursprünglich ihren Klimacharakter erworben. Sie wurden im Untersuchungsgebiet mit der holozänen Aufwärmung rasch und annähernd gleichzeitig eliminiert.
2. Arten der gemäßigten Holozänfauna. Sie erscheinen zeitlich gestaffelt im Holozän, einige wenige lassen sich auch im Jungpleistozän nachweisen.
3. „Durchgehende“ Arten. An Beispielen wird gezeigt, daß zumindest einige davon nicht, wie meist angenommen wird, durch ihre ökologische Valenz die biologische Caesur an der Pleistozän-Holozän-Grenze überdauerten, sondern kaltsteppenangepaßte Arten von den heutigen abgelöst wurden. Im Gegensatz zur Gemeinschaft der Gruppe 1 waren die jungpleistozänen Arten der Gruppe 3 wahrscheinlich auf den Westen der Palaearktis beschränkt und mußten dementsprechend hier im Jungpleistozän ihren Klimacharakter erworben haben. Sie bestehen heute nicht mehr.

Summary

The small mammal fauna of southern Germany during the pleistocene-holocene-boundary

The climatic change at the pleistocene-holocene-boundary was very sudden and severe in the region under study. The small mammal fauna of this period can be arranged in three groups:

1. Species of the upper pleistocene cold steppes. They persist in their continental holarctic areas where they acquired their ecological characters, and from where they penetrated our region. They became extinct very rapidly and nearly all rather contemporarily.
2. Species of the temperate holocene fauna. They appear successively during the lower holocene: few of them have been found also during the upper pleistocene.
3. Species which were often thought to be identical as well in upper pleistocene as in holocene faunas. But examples demonstrate that at least some of them have not persisted the severe biological cut: cold adapted species were replaced by the recent ones in these cases. Contrarily to the species of group 1 the upper pleistocene species of group 3 were restricted to the western palaeartic. Here they must have acquired their ecological characters. They did not survive to recent times.

Literatur

- BOBRINSKIJ, N. A.; KUSNEZOV, B. A.; KUSJAKIN, A. L. (1965): Bestimmungsschlüssel der Säugetiere der UdSSR. Moskau.

- CHALINE, J. (1972): Le Quaternaire — L'Histoire humaine dans son environnement. Paris.
- FAHLBUSCH, V. (1970): In KOENIGSWALD, W. v.: Mittelpleistozäne Kleinsäugerfauna aus der Spaltenfüllung Petersbuch bei Eichstätt. Mitt. Bayer. Staatssamml. Paläont. hist. Geol. 10, 407—432.
- FIRBAS, F. (1952): Spät- und nacheiszeitliche Waldgeschichte Mitteleuropas nördlich der Alpen. 2, Jena.
- FRENZEL, B. (1967): Die Klimaschwankungen des Eiszeitalters. Wissenschaft 129, Braunschweig.
- (1968): Grundzüge der pleistozänen Vegetationsgeschichte Nord-Eurasiens. Erdwiss. Forschung 1, Wiesbaden.
- GROMOV, I.; BIBIKOV, D.; KALABUCHOV, N.; MEIER, M. (1965): Fauna SSSR: Säugetiere 3, Marmotinae. Moskau, Leningrad.
- GUILDAY, J. E. (1967): Differential extinction during late-pleistocene and recent times. In MARTIN, P. S.; WRIGHT, H. E. (ed.): Pleistocene extinctions. The search for a cause. New Haven and London.
- GUTHRIE, R. D. (1968): Paleocology of a Late Pleistocene small Mammal Community from Interior Alaska. Arctic 21, 223—244.
- HEIM DE BALSAC, H.; GUISLAIN, R. (1955): Evolution et spéciation des campagnols du genre *Arvicola* en territoire Français. Mammalia 19, 367—390.
- HELLER, FL. (1955): Die Fauna. In ZOTZ, L. F.: Das Paläolithikum in den Weinberghöhlen bei Mauern. Quartär-Bibl. 2, 220—307.
- HINTON, M. A. C. (1926): Monograph of the voles and lemmings (Microtinae) living and extinct. Vol. I. London.
- JÁNOSSY, D. (1961): Die Entwicklung der Kleinsäugerfauna Europas im Pleistozän (Insectivora, Rodentia, Lagomorpha). Z. Säugetierkunde 26, 1—11.
- LANG, G. (1952): Zur späteiszeitlichen Vegetations- und Florengeschichte Südwestdeutschlands. Flora 139, 243—294.
- MANDACH, E. v. (1927): Die kleineren Wirbeltiere der prähistorischen Station „Bsetzi“ bei Thayngen (Kanton Schaffhausen) Schweiz. Ber. naturforsch. Ges. Freiburg i. Br. 27, 97—143.
- (1930): Die kleineren Wirbeltiere. In PETERS, E.: Die altsteinzeitliche Kulturstätte Petersfels. Augsburg.
- MOREAU, R. E. (1955): Ecological changes in the Palaearctic Region since the Pliocene. Proc. zool. Soc. London, 125, 253—295.
- REICHSTEIN, H. (1963): Beitrag zur systematischen Gliederung des Genus *Arvicola* LACEPEDE 1799. Z. zool. Syst. Evolut.-forsch. 1, 155—204.
- SOERGEL, W. (1940): Zur biologischen Beurteilung diluvialer Säugetierfaunen. Sb. Heidelberg. Akad. Wiss., math.-nat. Kl. 1940 4, 1—39.
- STEHLIN, H. G. (1932, 1933): In DUBOIS, A.; STEHLIN, H. G.: La grotte de Cotencher, station moustérienne. Mém. Soc. pal. suisse 52, 1—178 (T. I), 53, 179—292 (T. II).
- STEIN, G. (1963): Unterartengliederung und nacheiszeitliche Ausbreitung des Maulwurfs, *Talpa europaea* L. Mitt. zool. Mus. Berlin 39, 379—402.
- STORCH, G. (1969): Über Kleinsäuger der Tundra und Steppe in jungpleistozänen Eulengewölkern aus dem nordhessischen Löß. Natur und Museum 99, 541—551.
- (1971): Die Pleistozän-Holozän-Grenze bei *Arvicola* in Süddeutschland. Vortrag, gehalten auf dem Symposium theriologicum, Brno CSSR.
- (1972): In BESENECKER, H.; SPITZENBERGER, F.; STORCH, G.: Eine holozäne Kleinsäugerfauna von der Insel Chios, Ägäis. Senckenbergiana biol. 53, 145—177.
- (1973): Jungpleistozäne Kleinsäugerfunde (Mammalia: Insectivora, Chiroptera, Rodentia) aus der Brillenhöhle. Forsch. u. Ber. Vor- u. Frühgesch. Baden-Württemberg 4.
- TOBIEN, H. (1939): Die Kleinsäugerreste aus der Falkensteinhöhle im oberen Donautal. Bad. Geol. Abh. 10, 126—130.
- Vegetationsgeschichtliches Symposium im Rahmen der Tagung der Deutschen Botanischen Gesellschaft, Innsbruck 1971. Ber. deutsch. botan. Ges. 85, H. 1—4.
- VOGEL, R. (1940): Die alluvialen Säugetiere Württembergs. Jh. Ver. vaterl. Naturkde. Württ. 96, 89—112.
- WERTH, E. (1936): Der gegenwärtige Stand der Hamsterfrage in Deutschland. Arb. biol. Reichsanst. Land- u. Forstwirt. Berlin 21, 201—253.
- WETTSTEIN, O. v.; MÜHLHOFER, F. (1938): Die Fauna der Höhle von Merkenstein in N.-Ö. Arch. Naturgesch., N.F. 7, 514—558.
- WOLDRICH, J. N. (1893): Reste diluvialer Faunen und des Menschen aus dem Waldviertel Niederösterreichs. Denkschr. kaisl. Akad. Wiss., math.-nat. Kl. 60.
- WOLDSTEDT, P. (1969): Quartär. Handb. stratigr. Geol. 2. Stuttgart.

Anschrift des Verfassers: Dr. G. STORCH, D—6000 Frankfurt a. M., Forschungsinstitut Senckenberg, Senckenberganlage 25

Investigations on the Sciurid manus

I. Some new taxonomic characters and their importance in the classification of squirrels

By CHARLES A. LONG and JOSEPH CAPTAIN

Receipt of Ms. 28. 1. 1973

Introduction

The structure of the manus is important in the classification of the Sciuridae. Some of the characters of the manus that distinguish high taxonomic groups result perhaps from evolutionary convergence, but others are conservative and useful. Some trends in form of the manus are irreversible, and therefore reveal phylogenetic information.

The characters of the forefoot augment those of the teeth and baculum in sciurid classification.

Materials and methods

The forefoot of specimens in Nearctic *Eutamias* (*minimus* 32, *amoenus* 2, *dorsalis* 2, *merriami* 1, *ruficaudus* 1, *quadrivittatus* 2, *umbrinus* 9, *ruficaudus* 1), *Tamias striatus* 86, *Marmota* (*monax* 5, *flaviventris* 2), *Spermophilus* (*tridecemlineatus* 34, *spilosoma* 1, *mexicanus* 1, *franklinii* 5, *lateralis* 9, *tereticaudus* 3, *variegatus* 3, *armatus* 3, *richardsonii* 8, *beldingi* 1, *townsendii* 1, *washingtonii* 1, *beecheyi* 1, *undulatus* 1), *Ammospermophilus* (*leucurus* 1, *harrisi* 3), *Cynomys* (*leucurus* 3, *ludovicianus* 1), *Tamiasciurus* (*douglasii* 1, *hudsonicus* 70), *Sciurus* (*niger* 24, *carolinensis* 41), and *Glaucamys* (*sabrinus* 6, *volans* 22), as well as three Oriental species (*Petaurista lena* 1; *P. grandis* 1; *Sciurus lis* 1) and one South American species (*Sciurus granatensis* 2) was examined of preserved skins in the University of Wisconsin-Stevens Point Museum of Natural History. A skin of *Aplodontia rufa* was also examined. Representative skins obtained on loan of some genera of South American, African, and Asian squirrels were examined, including two *Microsciurus mimulus* (Colombia), two *Sciurotamias davidianus* (Wen Chuhn, China), two *Callosciurus caniceps* (Siam), two *Menetes berdmorei* (Viet Nam), one *Ratufa bicolor* (South Viet Nam), one *Reithrosciurus macrotis* (Borneo), two *Nannosciurus borneanus* (Borneo) one *Rhinosciurus laticaudatus tupaoides* (Malaya), two *Heliosciurus rufobrachium* (Ogouma, Africa), one *Myosciurus minutus* (Kamerun, Africa), two *Protoxerus stangeri* (Ogouma, Africa) and two *Epixerus wilsoni* (Pemba, Nyambi, Africa).

Results and discussion

Systematics of recent Sciuridae

The Sciuridae have received much attention from taxonomists and paleontologists (POCOCK, 1922, 1923; BRYANT, 1945; MOORE, 1959; WILSON, 1960; BLACK, 1963; and others). *Sciurus* is usually considered a generalized, primitive form. Subfamilies listed in BLACK are Sciurinae and Petauristiae. The former includes the tribes Tamiini (chipmunks), Sciurini (*Sciurus*, *Tamiasciurus*, and other scansorial forms), Funambulini (*Myosciurus*, *Funambulus*, etc.), Callosciurini (numerous diverse genera such as *Callosciurus*, *Nannosciurus*, *Menetes*, *Sciurotamias*), Marmotini (holarctic ground

squirrels and marmots), and Xerini (African ground squirrels). The Petauristinae contains a dozen genera of volant squirrels.

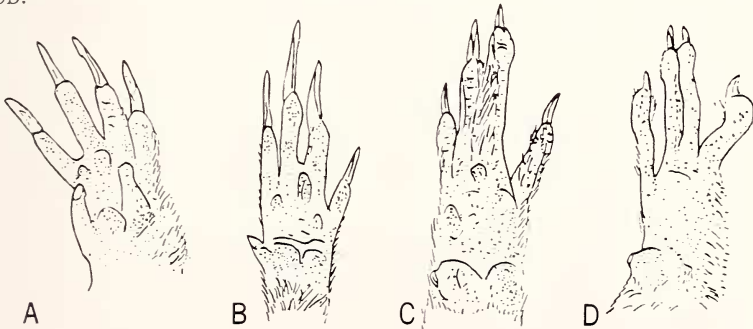
Many modern workers have removed *Tamiasciurus* from Sciurini (MOORE, 1959) chiefly because its simple penis usually lacks a baculum. MOORE arranged *Tamiasciurus* with *Sciurotamias*, but BLACK placed the latter in the Callosciurini. BLACK doubted that the Petauristinae is a natural group, and stated that the group arose from "tree squirrels", probably *Sciurus* and *Callosciurus*. The recent taxon closest in relationship to the Sciuridae is the exceptionally primitive Aplodontidae of the American Northwest.

Patterns and characters

Study of the sciurid forefoot reveals important patterns and new characters, some of which are phylogenetically irreversible.

The sciurid manus functions in digging, holding food, scampering, climbing, grooming and copulation. No generalizations seem to have been recorded regarding structure of the sciurid foot excepting comments on the elongation of the bones of the limb and manus in arboreal and flying squirrels (PITERKA, 1936; BRYANT, 1945) and an observation that some squirrels are "perissodactyl" in having the third digit longest whereas others are "artiodactyl" having the third and fourth nearly equal, the fourth slightly longer (POCOCK, 1922). POCOCK and others have mentioned that squirrels generally have a nail on the first digit, and BRYANT stated that all Nearctic squirrels possess one excepting *Cynomys*, which has a stout claw.

WOOD (1962) described the partially complete manus in several paramyid (= ischyromyid) fossils. In *Leptotomus* the thumb seemed "divergent", and the pattern of the digits was problematic though metacarpals III and IV were subequal. In *Ischyrotomus* IV was elongate but III possibly longer, and the thumb appeared robust. In *Pseudotomus* the "strongly divergent" thumb was robust and freely movable. The third digit was longest and IV was longer than II, which exceeded V in length. The elongate digit III is unlike that of modern arboreal squirrels. Probably some ancestral squirrels and certainly some ancestral rodents (ischyromyids) were semi-arboreal, showing some scansorial adaptations such as elongate tail according to WOOD.



Manus in some sciuiromorph rodents. A. *Aplodontia rufa*; B. *Spermophilus mexicanus*; C. *Sciurus carolinensis*; D. *Glaucomys volans*

Assuming semi-arboreal *Aplodontia rufa*, of the closely related and primitive Aplodontidae, has a primitive structure of the manus, then the ancestral sciurid foot was probably pentadactyl with the first digit functional and armed with a claw, the second digit longer than the fifth, and the third the longest (Fig.), as in *Pseudotomas*. This pattern is widespread in the Rodentia.

In burrowing ground squirrels and their allies (Marmotini) the first digit is extremely short, the third longest (perissodactyl), the second is longer than the fifth usually, and the small "nail" on the pollex is usually somewhat pointed (except in *Marmota*) (see Fig.). Fossorial mammals such as pocket gophers, badgers, and moles show a similar development of the second and third digits.

Tamias, *Eutamias*, *Tamiasciurus*, *Sciurotamias*, and *Rhinosciurus* have a generally artiodactyl pattern; the paired subequal digits (III, and IV, II and V) are not so specialized in elongation of the outermost digits as seen in the pattern of arboreal and volant species. All of these genera spend much time on the ground, and their taxonomic affinities with other sciurids are unknown. *Rhinosciurus* is extremely specialized for feeding on ants.

In the arboreal pattern, found also in the volant species, the fourth toe is markedly longer than the third. The rudimentary first digit bears a nail-like structure. The fifth toe, as well as the fourth, shows elongation, and they both ordinarily exceed the second in length (see Fig.).

The tendency to lengthen the lateral digits and relatively speaking to concomitantly suppress the inner ones is adaptive in a form which climbs vertical, cylindrical tree trunks. The arms and sharply clawed digits must encompass much of the curved surface to prevent the squirrel from falling backward.

Evolution of ancestral squirrels

The Sciuridae probably arose from the extinct Paramyidae (BRYANT, 1945; WILSON, 1949; BLACK, 1963), now regarded by BLACK (1971) as the Ischyromyidae. They show close resemblance to recent *Sciurus* in the pattern of the molar teeth (WOOD, 1962). WILSON (1960), BRYANT (1945), and BLACK (1963) suggest that the ancestral (Oligocene) squirrels were ground forms, although WILSON has discussed the popular acceptance of *Sciurus* as primitive. WOOD (1962) has shown semi-arboreal specializations in ischyromyids.

Evolution of ground squirrels

In North America *Tamias* is the oldest genus that survives today, closely related to *Protosciurus* (BLACK, 1963). *Spermophilus* appears in the record later, and *Marmota* even later. Our study of the manus shows *Marmota* to resemble *Spermophilus* and *Cynomys* in digital pattern, but the broad nail on the nearly vestigial pollex in marmots indicates some divergence from the spermophiles. The foot of *Cynomys* is advanced beyond that in *Spermophilus*, and this specialization is consistent with the hypothesis of NADLER et al. (1971) and BLACK (1963) that *Spermophilus* is the ancestor of *Cynomys*.

The marmots are interesting because their pattern of the manus resembles that of semi-fossorial *Spermophilus* and *Cynomys*, yet the pollex bears a broad "nail". *Marmota marmota* lacks the pollex and nail (POCOCK, 1922). The nail suggests a surprising affinity with tree squirrels or, much more likely, a general preference for boulders and other rocky habitats (for example, in *Marmota flaviventris* of the Rocky Mountains). In any event, the broad nail reveals a significant divergence from the holarctic ground squirrels and *Cynomys*. Assignment of all these terrestrial squirrels to the Marmotini is based chiefly on a strong resemblance of the baculum (POCOCK, 1923) and teeth (BLACK, 1963).

According to POCOCK (1923) the African ground squirrels, Xerini, have the middle digit longest, although IV is slightly longer than II. Thus, surprising convergence with the ground dwellers' pattern in the Marmotini is evident.